BEHAVIORAL ASYMMETRY IN RELATION TO BODY WEIGHT AND HUNGER IN THE TROPICAL SOCIAL SPIDER *ANELOSIMUS EXIMIUS* (ARANEAE, THERIDIIDAE)

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ABSTRACT. It has been hypothesized that larger females of the social neotropical spider *Anelosimus eximius* (Keyserling 1884) (family Theridiidae) take advantage of the food captured by smaller females, and thus maintain a higher social rank within a colony. To test this hypothesis, the behavior of adult females in three colonies of *A. eximius* was observed in the Panama rain forest. Adult spiders with low body weights did most of the building, cleaning and repairing of the communal web, while heavier spiders more often took care of egg sacs. The latter stayed mostly inside safe retreats while low-weight spiders were mostly outside the retreats, where mortality was high. Reproducing spiders were of high body weight.

To test whether this behavioral asymmetry is related to the nutritional condition of a female a manipulation experiment was conducted. A comparison of adult females, which were either well fed or starved, showed that starved females do more web maintenance, spend more time outside the retreats and more often take part in attacking prey. I conclude that both hunger (recent feeding success) and general nutritional condition (body weight) are the cues for the observed behavioral asymmetry in colonies of *Anelosimus eximius*. It is currently unknown whether the observed asymmetry is stable over time or whether it is age-related.

Sociality in spiders provides an interesting and challenging parallel to its evolution in other social organisms, in particular social insects (Wilson 1971). Among spiders a wide continuum of sociality from temporal aggregation up to permanent social colonies is found (Buskirk 1981). Although morphological castes have never been observed (e.g., Lubin 1995), it was suggested that a dominance structure exists in colonies of *Anelosimus eximius* Simon, which supposedly leads to an asymmetrical distribution of behavior (Vollrath 1986a). Since fewer egg sacs than adult females are found within these colonies, and the rate of insemination of adult females is low, Vollrath (1986a) speculated that a few, larger females suppress smaller colony members. It has been shown that in *A. eximius* that particularly large prey items lead to feeding and reproductive asymmetries within colonies (Rypstra 1993). As a possible mechanism for this asymmetry, Vollrath (1986a) speculated that females take advantage of prey caught by smaller colony members. Thus, small spiders would conduct the dangerous task of prey cap-

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ture while larger females reproduce. However, reproductive asymmetry could simply be due to the presence of some larger spiders which hunt more successfully, eat more prey and eventually gain enough resources to reproduce, while others are never able to reproduce. To understand whether reproductive asymmetry exists in natural colonies of *A. eximius* and, if so, how it is maintained, I investigated the behavior of adult *A. eximius* females in relation to spider size and hunger in three colonies in the Panama rain forest.

Colonies of the social spider *A. eximius* occur in neotropical rain forests from Panama to southern Brazil (Levi 1956, 1963) and are typically found in bushes or trees along roads, in forest gaps or in open habitat close to rain forests. Colonies may contain a few, or up to several thousand members, with overlapping generations (Christenson 1984; Vollrath 1986b, but see Avilés [1986] for possible exceptions) and cooperative care of brood (Vollrath & Rohde-Arndt 1983; Christenson 1984). The web consists of a basket-like sheet inside of which fallen leaves are used as retreats. Above the sheet is the snare, an irregular structure of non-sticky silk threads, which acts

to catch prey (see drawings in Vollrath [1982] and Christenson [1984]). Prey are attacked by one or several spiders and transported into a nearby retreat where feeding takes place. Communal attacks allow for capture of prey several times the size of adult spiders (Nentwig 1985; Rypstra 1990; Pasquet & Krafft 1992). Males rarely contribute in social activities. Sex ratio within colonies is strongly female biased (Avilés 1986; Vollrath 1986a) and as in other highly social spiders (Roeloffs & Riechert 1988), colonies are highly inbred (Vollrath 1982; Smith 1986). Both sexes are diploid (Vollrath 1986a).

Apart from prey capture and handling, colonies show a distinct bimodal daily activity pattern (Christenson 1984; Pasquet & Krafft 1992; D.E. pers. obs.). During both day and night hours most spiders stay motionless either close to or inside the retreats, although some females may feed spiderlings or clean egg sacs. Around sunrise and sunset, web maintenance activity (i.e., repair), cleaning and construction of snare and sheet, peaks for 1–2 hours.

METHODS

Anelosimus eximius colonies were found in Central Panama along El Llano-Carti Road, (2 miles south of Kuna Station, 78°57′W, 9°20′N), along a rainforest road close to the Atlantic coast (79°58′W, 9°25′N) and along the road to the highest elevation on Taboga Island (Pacific Ocean, off shore Panama City, 79°33′W, 8°47′N). Central Panama has a pronounced seasonality, with a dry season from December until May, during which insect abundance, and thus spider food, is lower than during the rainy season (Wolda 1978; Vollrath 1986a). My study was conducted from mid-December 1991 until mid-February 1992. On six days field work was interrupted by rain.

Observation of marked spiders was only possible by placing colonies into small isolated bushes, a treatment which seems not to affect the spiders' behavior (Vollrath & Rohde-Arndt 1983; Christenson 1984). Of nine colonies moved (with 15–25 adults and about 10–100 juveniles each), seven re-established new webs within the first night, while in two cases most spiders disappeared within the first night. Colonies were allowed to establish for one week. The new colonies had a diameter of 20–30 cm and the snare reached up to 60

cm in height. Natural colonies with similar numbers of females are in approximately the same size range (D.E. pers. obs.). In some cases I had to remove fallen leaves to allow free observation. Six of the seven colonies were used during the study. Experimental colonies were located in a tree gap along pipeline road (Parque Nacional Soberania, 79°45′W, 9°10′N) in a tropical lowland rainforest, an area suitable for *A. eximius* (Vollrath 1986b). All colonies were located within an area of 15 m diameter. No egg sacs were present in these colonies at the start of the study.

Estimation of nutritional conditions.— Cephalothorax width of 201 females from five natural colonies was measured to the nearest 0.01 mm using a dissecting microscope with ocular micrometer. The largest class of approximately normally distributed widths (1.27–1.59 mm) did not overlap with the size class of the penultimate instar (0.97–1.25 mm), allowing for reliable distinction between adult and sub-adult females.

In contrast to the cephalothorax, which is fixed by instar, the abdomen is distensible and increases in volume during feeding or egg production, allowing for assessment of nutritional condition without disturbing the spider (Anderson 1974; Foelix 1985). I classified abdomen-size of adult females according to classes from 1 to 9, where 1 represents the smallest (rod-shaped abdomen) and 9 represents the largest abdomen (egg-shaped). These classes were compared with body fresh-weight and cephalothorax width of 51 adult females.

Colony observation.—For 30 days three experimental colonies were observed for 2–8 successive hours per day (mean = 4.8 h/day), usually from early afternoon to 1800 h. Cumulative observation time was more than 100 h per colony. *A. eximius* shows two activity peaks per day, around sunrise and around sunset. Most observations on web maintenance activity are done around sunset, which might bias these data. However, on three occasions early in the study I observed spiders from 0600–0800 h and compared their activity with the evening activity. Since activity levels appeared not to differ between morning and evening observations, I studied web maintenance activity only in the evening.

All adult females were individually marked with a code of four non-toxic colors on ab-

domen and legs. These marking are perma-
nent, since adult spiders do not molt anymore.
At the beginning of the observation period
each day, I recorded the presence of adult fe-
males, females which had molted recently into
the adult stage, number of egg sacs, and the
length and number of prey carcasses. I further
classified abdomen-size of each adult female.
Bodies of dead females were removed from
colonies and cephalothorax width was mea-
sured.

At 10 minute intervals I recorded the lo-
cation (inside or outside retreat) and behavior
of every marked individual. Juveniles and
males were ignored. A female was considered
to be outside the retreat when her legs touched
the threads of the snare directly and she was
not located under a leaf. I distinguished the
following behaviors: web maintenance (repair,
cleaning and construction of snare and sheet),
care of egg sacs (guarding and cleaning of egg
sacs), feeding on prey and motionless waiting.
I estimated body length of prey in relation to
adult female body length (about 5 mm) and
noted the females which attacked, transported
and fed on the prey. Prey length and the
marked attacking females were also recorded
when prey escaped during attack. Although
prey length may be a poor predictor of prey
weight, (some prey may be short and fat,
whilst others are thin and long) over the whole
range of prey observed (about 1–25 mm) prey
length is likely to be a good predictor of
weight.

Food restriction experiment.—From ex-
perimental colonies 4, 5 and 6, I removed six
adult females each, marked and kept them in
two groups in 20 × 30 × 40 cm cages. One
cage was used for each treatment group and
each colony ($n = 6$). For one week, three fe-
males from each colony were starved while
the others were fed twice a day (around 0900
and 2000 h) with flies, wasps and grasshop-
pers caught around the colonies. To assign fe-
males to the starvation or feeding treatment I
caught them one by one and tossed a coin. All
cages were sprinkled with water twice a day.
All 18 spiders (3 colonies × 2 treatments ×
3 females) survived. After one week spiders
were placed back into their home colonies at
1800 h. The following three days I recorded
the behavior of these spiders in each colony
from 1200–1800 h.

Data analysis.—Data on spider location

(inside or outside retreat) were used only for
time periods between 0800–1700 h (inactive
period, Pasquet & Krafft 1992). Data on web
maintenance were used only between 1700–
1800 h (active period) because web mainte-
nance behavior was only observed during
hours of changing daylight and because spider
location and web maintenance were not in-
dependent (during web maintenance a spider
is always outside the retreat). The times for
egg care and web maintenance behavior, as
well as the time spent inside or outside the
retreats were calculated for each female as
proportion of the daily observation period. For
these calculations I did not consider times dur-
ing which at least one female was involved in
attacking or transporting prey and the first
hour of feeding on prey. Egg care behavior
was analyzed only for those days when at
least one egg sac was present in the colony.
Proportions were square-root arcsin trans-
formed and tested for normality (SAS Inc.,
1990).

The abdomen-size classes are ordinal num-
bers and can therefore be used in parametric
analysis only with caution. However, a re-
gression of body-fresh-weight on the abdo-
men-size class of 51 adult females showed
that the abdomen-size classes are very well
linearly correlated with body-fresh-weight
(see Results section). Therefore, I used ab-
domen-size estimates in analysis of covari-
ance (ANCOVA) as covariable. These AN-
COVA's tested for the dependence of web
maintenance behavior, attacking frequency,
proportion of time a spider stayed inside the
retreat and the proportion of time caring for
egg sacs on abdomen-size. To linearize the re-
lation between the dependent variable and the
covariable, I used the square-root of abdomen-
size in the ANCOVAs of web maintenance
and location, and the square of abdomen-size
in the ANCOVAs of attacking frequency and
egg caring. These four ANCOVA's included
further colony and individuals as factors, with
individual females nested within colonies and
repeated observations on females nested with
individuals. Colonies were tested over indi-
viduals. Type III sum of squares were calcu-
lated because the number of females was not
equal within the three colonies (Procedure
GLM, SAS, Inc, 1990).

RESULTS

Spider abdomen-size.—From 51 adult spiders a correlation between cephalothorax width, abdomen-size classification and body fresh weight was done. Cephalothorax width was poorly correlated with body fresh weight (Spearman rank correlation: $r_s = 0.288$, $P < 0.05$), and not correlated with abdomen-size class ($r_s = 0.017$, $P > 0.8$). The nine abdomen-size classes however, correlated nicely with body fresh weight ($r_s = 0.88$, $P < 0.0001$). A linear regression relating fresh weight to abdomen-size class gave the following equation: weight[mg] = 5.88 + 1.715 × size-class.

To test whether the abdomen-size classification is a suitable predictor of body fresh weight under field conditions, I calculated the change in abdomen-size class from each pair of abdomen-size class for each female observed on two successive observation days. The abdomen-size class of those spiders which were observed feeding for at least one hour increased significantly compared to those who had not fed for at least one hour (colony 1: difference of the mean size class change of feeding and no-feeding females = 0.47, $P < 0.0001$, $df = 240$; colony 2: diff. = 0.31, $P < 0.05$, $df = 174$; colony 3: diff. = 0.72, $P < 0.0001$, $df = 136$; t-tests; with the number of degrees of freedom corrected for repeated measures of some individuals: $P < 0.01$, $P = 0.06$, $P < 0.001$, respectively; comparisons were done excluding females within a period of three days before or after egg laying). I conclude that the abdomen-size classification method is appropriate to estimate spider fresh weight by viewing their abdomen-size while in colonies.

Mean abdomen-size did not differ among the three colonies (Fig. 1), although females differed within colonies. The mothers with the seven egg sacs (five sacs were newly found in colony 1 and one each in colonies 2 and 3) had the largest abdomens. Abdomen-size dropped drastically after the eggs were laid (Fig. 1). Fourteen females which disappeared for unknown reasons had significantly smaller abdomens than the egg-laying females after eggs had been laid ($t = 3.01$, $P < 0.05$). The egg-layers were also larger than 10 females which were found dead hanging in the web ($t = 7.8$, $P < 0.001$). These latter females had
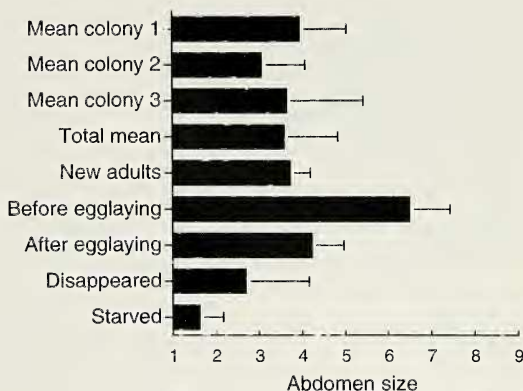

Figure 1.—Mean abdomen sizes (± 1 SD) of adult females. Except for the three first estimates, data were pooled from the three colonies. Categories: total mean = mean abdomen size of all females; new adults = females which molted during the previous day into the adult instar; before and after egg laying = females on the day before and the day after they laid an egg sac, respectively; disappeared = last size estimate of females which disappeared for unknown reasons; starved = females which were found hanging dead in the web.

shown a gradual decrease in abdomen-size before their death, although their cephalothorax widths were within the range of adult females (mean 1.423, SD = 0.07). If their bodies were not removed from the web, they were taken by ants. It is not clear whether these females died because of old age or because they starved. Five females molted into the adult instar during the study. The mean abdomen-size of these "new adults" at the first day of adulthood was not different from the average female size (Fig. 1).

It is possible that spiders of the last juvenile instar were mistaken as adults, since the largest juveniles are nearly as large as small adults. However, I believe the chances for this mistake are very low. First, I observed no case in which an adult female disappeared and a new adult appeared at the same time, which would happen if a large juvenile (mistaken as adult) molted to become adult. Second, at the end of the study all marked females were taken to the laboratory and their cephalothorax widths measured. All widths were well in the range of widths determined earlier for adult females.

Abdomen-size and behavior.—Web maintenance behavior and prey-attacking frequency decreased with increasing abdomen-size,
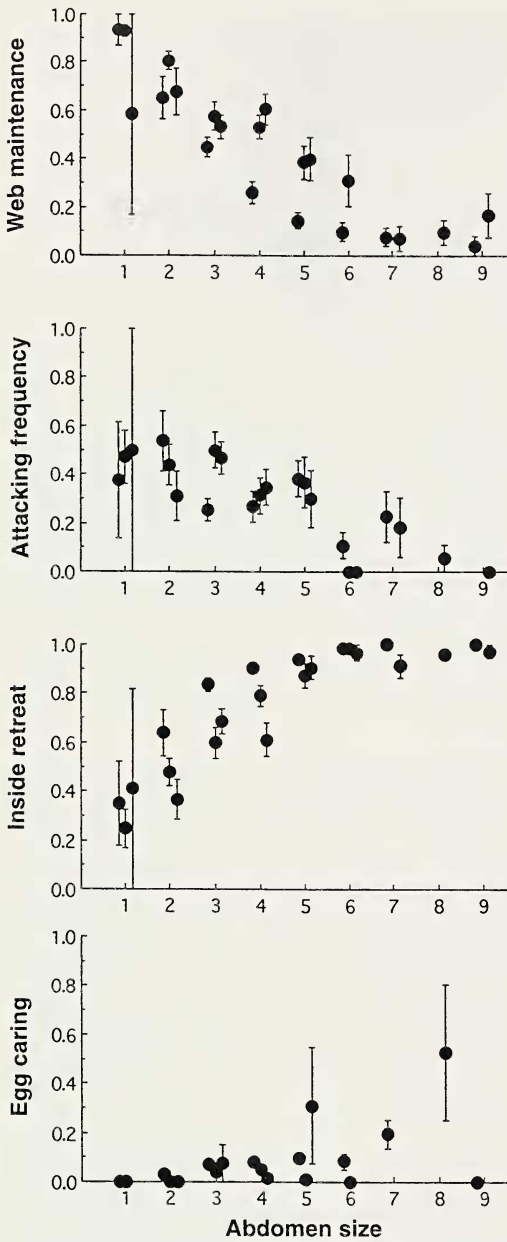
Figure 2.—Proportion of females (± 1 SE) showing four behavioral traits in relation to their abdomen size. Behavioral traits are the proportion of time a female does web maintenance, the proportion of females taking part in attacking prey, the proportion of time a female stayed inside the retreats and the proportion of time a female cares for eggs. Each point represents the mean of all females of each colony in the corresponding size class. To avoid overlap, means of colony 1 were shifted 0.15 size classes to the left and means of colony 3 were shifted 0.15 size classes to the right. Only points are included which represent the mean from at least two observations. Note that for some means the error bars fall within the dots.

while the tendency to stay inside the retreats and to care for egg sacs increased with increasing abdomen-size (Fig. 2, Table 1). No correlation was found for the relation between feeding time and abdomen-size (Spearman, $P > 0.3$). Further, Vollrath's (1986a) speculation that feeding time should be inversely related with attacking frequency was not confirmed here (correlation between mean feeding time and mean attacking frequency per female: $r = -0.04$, 0.21 and 0.18 for colonies 1, 2 and 3, respectively; $P > 0.5$). There was an inverse relation between mean feeding time and mean web maintenance frequency (Fig. 3; colony 1: $r_s = -0.66$, $n = 18$, $P < 0.005$; colony 2: $r_s = -0.46$, $n = 15$, $P < 0.1$; colony 3: $r_s = -0.66$, $n = 10$, P < 0.05).

Prey size and spider behavior.—The number of females attacking prey and the

Table 1.—Nested analysis of covariance (ANCOVA) for four behavioral traits (compare Fig. 2). Individual females were nested within colonies, repeated measures of individual females nested within females.

| Source	df	type-III SS	F	P
Web maintenance behavior ($r^2 = 0.53$)				
colony	2	2.5709	1.66	0.20
individuals	46	35.6073	4.57	0.0001
size	1	5.5916	32.99	0.0001
size*colony	2	1.4101	4.16	0.016
error	522	88.4777		
Attacking frequency ($r^2 = 0.24$):				
colony	2	4.6714	2.37	0.073
individuals	46	38.8703	2.23	0.0001
size	1	2.0035	5.28	0.022
size*colony	2	3.9087	5.15	0.006
error	419	158.901		
Location of spider (inside retreat) ($r^2 = 0.50$):				
colony	2	4.0969	2.69	0.078
individuals	45	34.2601	5.32	0.0001
size	1	8.1441	56.94	0.0001
size*colony	2	3.3211	11.61	0.0001
error	570	81.5221		
Egg care frequency ($r^2 = 0.26$):				
colony	2	1.0652	4.64	0.015
individuals	40	4.5868	2.08	0.0002
size	1	0.2282	4.14	0.04
size*colony	2	0.4887	4.44	0.012
error	419	23.0815		
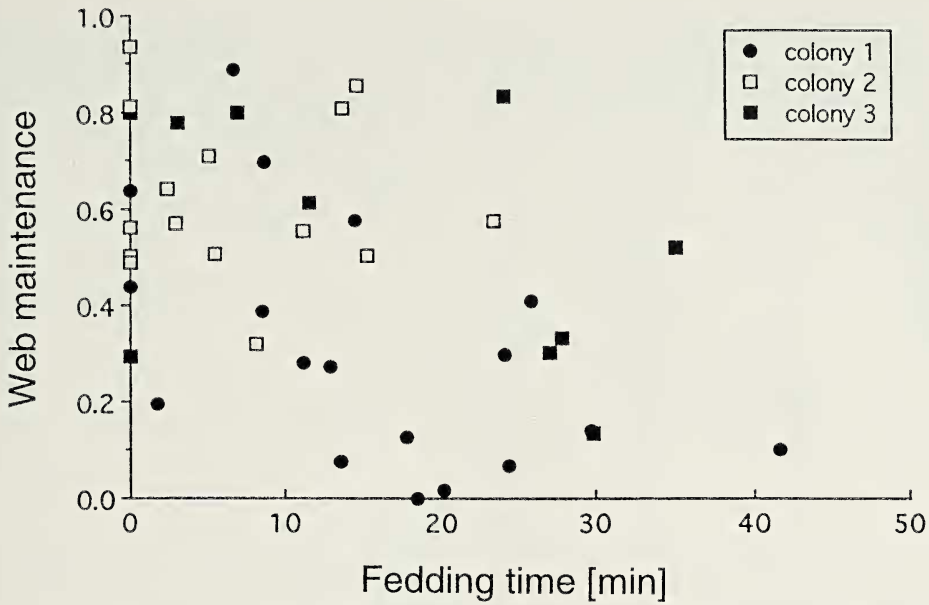
Figure 3.—The relation of mean female feeding time and web maintenance frequency. Each point represents the mean of one adult female, which was observed for at least five days. Feeding time represents the mean time a female spend feeding on one prey item. Pearson correlation coefficient for the pooled data: $r = -0.47$ ($P < 0.002$, $n = 43$).

number of females feeding on the captured prey increased with prey size (Table 2). The same is true for the number of females feeding without prior participation in attacking. Such opportunistic feeders are under represented when prey size is small, but are common for larger prey items (Fig. 4). Visualization of all four regressions in Table 2 suggests approximate linear relationships, although given the small sample size and the relatively low r^2 values non-linearity would be very difficult to detect.

About 50% of feeders on small prey (< 8 mm) had been outside the retreats at the moment the prey came into the snare (Fig. 5). For larger prey, almost all the spiders which took part in feeding were inside the retreats

when the prey came in (Fig. 5). The exceptional increase for the largest prey class in Fig. 5 is explained by the fact that in two cases the prey was so large that all adult females were able to take part in feeding. In summary, when food items are small, they were in many cases caught and eaten by females which waited outside the retreats. In contrast, larger prey were caught by all spiders (regardless of whether they were inside or outside the retreat when the prey came in), but were mainly eaten by those spiders which came from inside the retreat to join the attack.

Since spiders outside of retreats took part in most attacks, their under-representation among feeders on large prey requires an explanation. In 8 of 9 observed cases of direct

Table 2.—Regression of various measures of participation in prey handling on the size of prey (mm). Feeding time is the time from start of feeding on the prey until the last female left the prey. Data from all three colonies were pooled. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

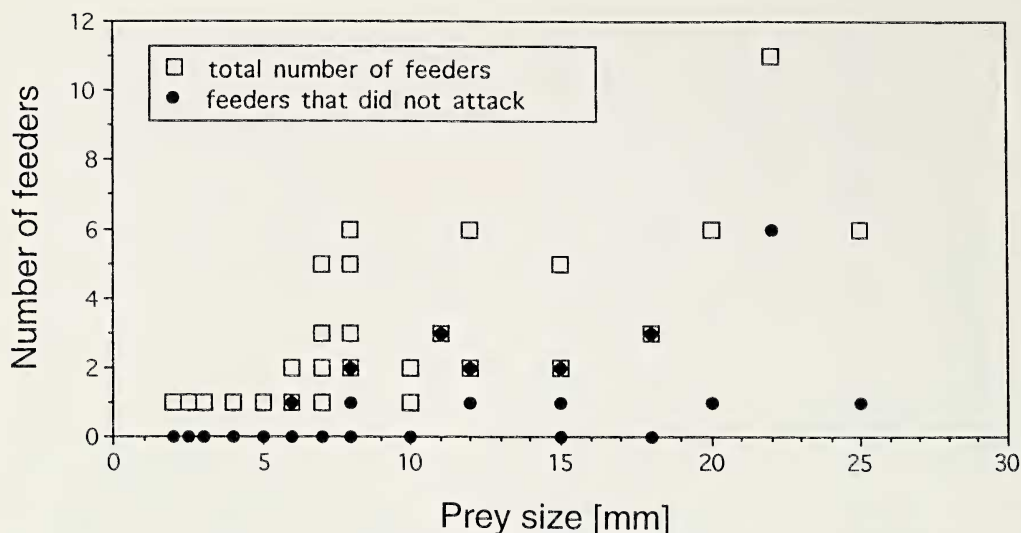| Trait	Intercept	Slope	r^2	n
Feeding time [min]	−0.438	0.374	0.58***	43
Total number females attacking prey	1.966	0.223	0.23**	44
Total number feeders on prey	0.698	0.227	0.38***	48
Number of feeders which did not attack prey	−0.502	0.128	0.33***	42

Figure 4.—Total number of feeders and number of feeders which did not take part in attacking prey (opportunistic feeders), in relation to prey size. Points are only included when the number of feeders were precisely known. Note that for small prey items (< 6 mm) no opportunistic feeders were observed.

interaction between two adult females over prey, abdomen-size class taken before the interaction was observed differed. In 7 of these 8 cases the larger female won the feeding position on the prey (paired *t*-test for size difference: diff. = 1.33, SE = 0.44, $P < 0.05$).

Mortality.—During this study I observed nine females killed by predators (1 giant damselfly, 1 mantid, 1 wasp, 4 jumping spiders, 2 orb-web spiders), whilst outside the retreats in the more peripheral parts of the colonies. All 9 were outside the retreat when captured; 6
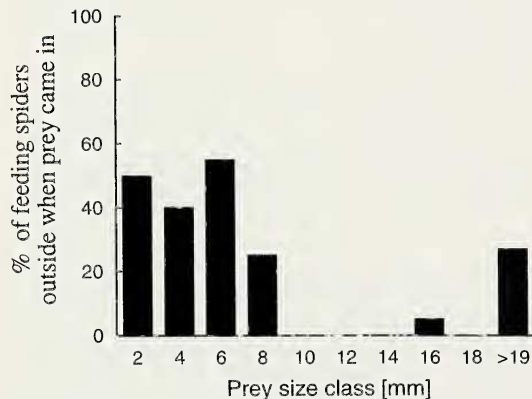

Figure 5.—Percentage of females taking part in feeding, which were outside the retreat at the moment prey of a given size class came in. Total sample size is 131.

died during web maintenance, 3 while waiting in the snare for prey.

Food restriction experiment.—The role of hunger in creating an asymmetric distribution of behavior was tested by the re-introduction of well-fed and starved females into their original colonies. The starved females spent on average 65% more time outside the retreats than the well-fed females and participated 33% more in web maintenance (Table 3). Starved females tended to attack more, regardless of whether they were inside or outside the retreats at the moment the prey came in (Table 3). This was found even if only those spiders that were inside the retreats when the prey came in were included in the analysis (Table 3). Not enough data were collected in this experiment to make a meaningful analysis with respect to feeding time.

DISCUSSION

Behavioral asymmetry and body size structure.—Short-term observation of individually marked adult females showed that behavioral asymmetry exists in the colonial spider *Anelosimus eximius*. This asymmetry seems to be governed by differences in body weight and hunger status. As already recorded by Vollrath & Rohde-Arndt (1983) only females of high body weight reproduce. In contrast, females with small abdomens conduct

Table 3.—Comparison between well-fed and starved females. Behavioral means represent the mean proportion of each of the three females for each of three days. Likelihood ratio tests (SAS Inc. 1990) were used to test frequencies of the given behavior against the alternative behavior (inside versus outside retreat, participation *versus* non-participation). $df = 1$ in all cases. A combined probability tests (Sokal & Rohlf 1981) combining the three colonies was significant for all 4 traits ($P < 0.01$).

Behavior	Colony	Fed	Starved	χ^2	P
Time outside retreat	4	0.068	0.955	171.6	0.0001
	5	0.189	0.973	137.9	0.0001
	6	0.676	0.973	25.9	0.0001
Participation in web maintenance	4	0.625	0.937	35.1	0.0001
	5	0.427	0.865	45.0	0.0001
	6	0.611	0.854	22.3	0.0001
Attacking	4	0.167	0.500	2.84	0.09
	5	0.091	0.615	7.73	0.005
	6	0.111	0.667	12.64	0.0001
Inside and attack	4	0.182	0.500	1.42	0.23
	5	0.111	0.500	3.23	0.07
	6	0.063	0.625	8.93	0.003

most of the web maintenance and usually stay outside the retreats. They take part in most prey-attacks, but feeding is limited to small prey items. Females of intermediate weight (i.e., abdomen-size classes 4–5) spend most of their time in the retreats, contribute little to web maintenance but take part in attack and feeding of larger prey items. By these means they may gain enough resources to become large and to reproduce. The largest females rarely take part in attacking or web mainte-nance, rarely leave the retreats, but do most of the egg sac care. These large, competitive females gain access to food by joining feeding companies or chasing smaller spiders away, as proposed by Vollrath & Rohde-Arndt (1983), Vollrath (1986a) and Rypstra (1993).

The altered behavior of large (size classes 5–9) females is not very surprising, given a high likelihood that they will lay eggs soon. Therefore this does not support the existence of a behavioral asymmetry. However, Fig. 2 shows that size related behavioral asymmetry is found even if only smaller size classes are considered. For example, the proportion of fe-males inside the retreats was about 30% for females of abdomen-size class 1 and about 70% for those of size class 4. Likewise, web maintenance behavior decreased from 75 to 50% from size classes 1 to 4.

The strong tendency for small, possibly less competitive, spiders to stay outside the re-treats may be explained as an optimal foraging strategy to gain access to at least some small food items, since females feeding on small prey were rarely joined by other females which did not take part in attacking (Fig. 4). Monopolization of small prey was also ob-served by Pasquet & Krafft (1992) for *Ane-losimus eximius* and by Brach (1977) for *A. studiosus* (Hentz 1850). Minute insects are sucked out on the spot by one or two spiders. The observation that small prey were ignored by *A. eximius* in laboratory colonies (Brach 1975) may be explained by the better nutri-tional status of laboratory spiders and a cor-respondingly higher threshold to response to web vibration (Vollrath 1986a). Small prey, e.g., small dipterans, generate less vibration than larger prey and may only be detected by spiders nearby, i.e., outside the retreat. This idea is supported by my observation that sometimes small insects caught in the periph-eral part of the web were not recognized by any of the females in the colony (D.E., pers. obs.). Alternatively, the low dry weight of small prey (Pasquet & Krafft 1992) might only be profitable for smaller spiders and are therefore ignored by larger colony mates.

The strong tendency of small spiders to stay outside the retreats may, however, be ex-plained as altruistic behavior, evolved to max-imize the success of the highly inbred colonies rather than the individual (Vollrath 1986a; Rypstra 1993). Individual selection on plastic-ity in foraging behavior in spiders with dif-ferent nutritional status might have pre-dated the evolution of sociality in spiders, suggest-

ing that the advantages of such plasticity for the colony could have played a role in the evolution of sociality as found in *A. eximius*.

Size-dependent behavioral asymmetry as described here has not been recorded in earlier studies. Vollrath & Rohde-Arndt (1983) reduced the body weight variance at the start of their study, which reduced the likelihood of detecting differences associated with body weight. The smallest females in my study were clearly of lower weight than females in the single colony of Vollrath & Rohde-Arndt (1983). The frequent occurrence of low body weights and general decline in my colonies might be a result of the poor feeding conditions during the dry season in Central Panama (Lubin 1978; Vollrath 1986b).

In summary, behavioral asymmetry with respect to prey-attack, web maintenance and reproduction is demonstrated by this study on three colonies of *A. eximius*. The data agree with earlier observations on the same species. The important question to ask now is whether a consistent size asymmetry is maintained over longer time periods.

Stability of size structure over time and food levels.—This study does not allow us to distinguish between a permanent size-structured behavioral asymmetry or a temporal (i.e., age related, Lubin (1995)) asymmetry. My study provides only a one month snapshot in time, which is shorter than the adult life span of *A. eximius* females. In the following I suggest four arguments in favor of a stable size (i.e., independent of the adult age of a female) hierarchy; however, it should be noted that only a much longer study will be convincing on this point.

First, the manipulation experiment with well-fed and starved females suggests however that age is of less importance. The experiment indicates that nutritional status explains a great deal of the observed behavioral asymmetry, although the remaining variance might well be age related.

Second, a positive correlation of spider size with feeding time could strengthen an existing size structure. Although my data do not support such a correlation, I believe that the true relationship between spider size and feeding success was underestimated. In contrast to small prey items, feeding time on large prey items was strongly underestimated because feeding often exceeded the observation period

and extended late into the night (D.E. pers. obs.; Rypstra & Tirey (1991)). Thus feeders joining the prey after the end of my observation periods escaped my attention. Reproducing spiders stop feeding a few days before they lay eggs (A.L. Rypstra pers. comm.), which reduces feeding time estimates of large spiders. Feeding time poorly estimates food uptake which varies in relation to prey size and the number of cofeeders, as shown for other colonial spiders (Ward & Enders 1985; Riechert et al. 1986).

Third, the relationship between spider size, behavior and prey size suggests that the stability of the female size hierarchy depends on the frequency and size of the incoming prey. In Panama, Peru and French Guiana it was found that in *A. eximius* colonies most prey was about 10–15 mm, which is 2–3× longer than adult *A. eximius* (Nentwig 1985; Rypstra 1990; Rypstra & Tirey 1991; Pasquet & Krafft 1992). Furthermore, 76% of incoming prey-dry-weight comes from prey items longer than 20 mm (Pasquet & Krafft 1992), suggesting that absolute feeding success of small females waiting outside the retreats for small prey is low so that changes in their relative position in the size hierarchy are less likely. Larger females get much more food by feeding on the larger and more common prey.

Fourth, from what was said before it appears that after periods of high prey capture success, even the smallest females might gain sufficient resources to become reproductive and thus overturn the reproductive asymmetry (Elgar & Godfray 1987). However, Rypstra (1993) showed in laboratory experiments that this seems to be the case only when prey is small. Strong asymmetry was observed when the spiders were fed exclusively on large prey. This indicates that food quality (size) but not quantity (number of flies) determines behavioral asymmetry in *A. eximius* (Rypstra 1993). An interesting point here is the observation that the size range of captured prey tends to increases with increasing colony size (Ward 1986; Pasquet & Krafft 1992). Thus, feeding asymmetry and the resulting reproductive asymmetry could be expected to become more pronounced as colonies grow.

In summary, stability of the size hierarchy in *A. eximius* colonies is likely to depend on the size structure of its natural prey. This problem can only be settled with more data

on the plasticity of lifetime reproductive success of individual spiders across the natural range of prey.

Mortality.—In colonies with high degrees of relatedness among colony members, strategies which maximize the survival of females at times when their reproductive value is high would be advantageous for the whole colony even if it reduced survival of non- or post-reproductive spiders (Wilson 1971; Jarvis 1981). All nine females which were seen to be captured by predators were located outside the retreats. It is not clear whether the web maintenance activity attracts predators, but a higher mortality risk on the periphery of a colony is reported from another colonial spider (Rayor & Uetz 1990). A higher mortality rate in females not involved currently in reproduction is indirectly supported by the finding that the 14 adult females which disappeared from the colonies were smaller on average than reproductive spiders. I suspect that these spiders became victims of predators rather than emigrated, because 1) I never found any marked spiders outside the colonies, 2) twice I found a single spider leg hanging in the snare after a spider disappeared, and 3) Vollrath (1982) reported that only females with swollen abdomens (presumably gravid females) emigrate, but the spiders which disappeared from my colonies were of small abdomen size (Fig. 1). In the light of this asymmetric mortality, future studies should include mortality in relation to attacking frequency (Vollrath & Rohde-Arndt 1983) and defense against intruders (Vollrath & Windsor 1986).

CONCLUSION

The social structure in colonies of *Anelosimus eximius* appears to be governed by behavioral asymmetry. This study shows that large competitive females reproduce, take care of egg sacs and avoid leaving the safe retreats. Small females do most of the foraging in terms of web maintenance, and have a higher risk of mortality by predators. The proximate cause of the asymmetry seems to be differences in nutritional condition and foraging behavior among females, as was shown in manipulation experiments with starved and well-fed spiders. Age effects could not be ruled out; however; the manipulation experiment showed that independent from the age of a female her nutritional status plays an im-

portant role. The ultimate cause might be that colonies with higher reproductive asymmetry produce more egg sacs then those with little or no asymmetry, suggesting that the maintenance of the size structure is beneficial for the whole colony (Rypstra 1993). More detailed studies on the food flow within colonies and observations over longer time periods are needed to predict who will be able to reproduce and whether the behavioral asymmetry is stable of time.

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